Substratal idiothetic navigation of rats is impaired by removal or devaluation of extramaze and intramaze cues

A. Stuchlik, A. A. Fenton, and J. Bures*

Institute of Physiology, Academy of Sciences, 14220 Prague, Czech Republic

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The spatial orientation of vertebrates is implemented by two complementary mechanisms: allothesis, processing the information about spatial relationships between the animal and perceptible landmarks, and idiothesis, processing the substratal and inertial information produced by the animal's active or passive movement through the environment. Both systems allow the animal to compute its position with respect to perceptible landmarks and to the already traversed portion of the path. In the present study, we examined the properties of substratal idiothesis deprived of relevant exteroceptive information. Rats searching for food pellets in an arena formed by a movable inner disk and a peripheral immobile belt were trained in darkness to avoid a 60° sector; rats that entered this sector received a mild foot shock. The punished sector was defined in the substratal idiothetic frame, and the rats had to determine the location of the shock sector with the use of substratal idiothesis only, because all putative intramaze cues were made irrelevant by angular displacements of the disk relative to the belt. Striking impairment of place avoidance by this ''shuffling procedure'' indicates that effective substratal idiothesis must be updated by exteroceptive intramaze cues.

It is generally believed that rodents are capable of constructing "cognitive maps" (1, 2), neural representations of spatial relationships between perceptible environmental landmarks. Such maps can provide an effective navigational mechanism requiring stability of landmarks (3) and sufficient time for learning their position in the charted environment (4). However, rodents can effectively orient in their habitat even when deprived of exteroceptive directional information. This ability is assumed to be implemented by idiothesis or path integration (4–9), i.e., by processing the information produced by the animal's active or passive movement, which can be gained in two different ways: (*i*) from the vestibular system measuring the inertial forces elicited by the concomitant accelerations (inertial idiothesis) and (*ii*) from proprioceptor signals and efference copies correlated with the subject's locomotion with respect to ground (substratal idiothesis). Integration of the above signals allows the animal to determine its position relative to a starting point. Inertial idiothesis is consistent with substratal idiothesis and exocentric orientation when the animal moves over a stable substrate, but the different navigation modes dissociate (7) during locomotion over moving ground or through moving substrate (air, water). Lesion studies (10–12) showed that landmark-guided navigation is primarily implemented by hippocampus, but the neural substrate of idiothetic navigation is still controversial (13, 14). Path integration research demonstrated that mammals are able to return directly to a starting point after an exploratory excursion in darkness (4, 13–15). Investigations of such homing tasks indicate that the reliability of path integration is limited by a cumulative error that must be corrected from time to time by referencing available allothetic information, e.g., azimuth of a distant landmark or known configuration of local landmarks (7, 9). A disadvantage of most homing studies is that they test path integration over short periods of time, not allowing the proper investigation of the influence of cumulative errors on the efficiency of idiothesis. This is why we developed a paradigm for testing path integration dissociated from reliable exteroceptive stimuli over an extended period. We set three basic criteria that our paradigm had to meet. (*i*) Any exteroceptive information should be eliminated or made irrelevant for the solution of the task. (*ii*) The duration of an experiment should permit the estimation of the longest time during which accurate navigation can be maintained by pure substratal idiothesis. (*iii*) The efficiency of path integration should be quantifiable by directly measurable parameters.

To match these requirements, we designed a task, based on the place avoidance paradigm (16–18), in which the rat collects food pellets scattered on a circular arena and simultaneously avoids a sector, entering of which is punished by mild electric foot shocks. The task can be carried out either in light or in darkness, on either a rotating or a stable arena, and the shock sector can be defined either in the reference frame of the room or in the coordinate system of the arena. Unlike in the original study, the circular arena consisted of an inner disk and a peripheral belt. Slow intermittent rotation of the disk inside the stable belt produced radial discontinuity of the arena surface. This procedure permitted us to make all exteroceptive cues, both extramaze (visual and auditory) and intramaze (olfactory and tactile), irrelevant for avoiding the shock. The rats thus had to localize the shock sector by pure substratal idiothesis, because relying on exteroceptive cues led to errors. Preliminary description of the shuffling procedure had already been presented (18, 19).

NEUROBIOLOGY

General Methods

Animals. Adult male Long–Evans rats ($n = 15$; 250–300 g; breeding colony of the Institute of Physiology, Academy of Sciences) were housed four in a plastic cage in a room with constant temperature (21°C) and a natural light/dark cycle. One week after surgery, food availability was gradually decreased to reduce the body weight to 85%; water was always freely available. The experimental procedures were in accordance with Czech laws and international guidelines for the protection of laboratory animals.

Surgery. Rats were anesthetized with Thiopental (VUAB, Prague, Czech Republic; 50 mg/kg i.p.), and a 4-cm-long, 0.2-mm-thick silver wire with a blunted tip was introduced beneath the skin of the neck and connected to a minisocket that was fixed to the skull by anchoring bolts and dental acrylate.

Abbreviation: LED, light-emitting diode.

*To whom reprint requests should be addressed at: Institute of Physiology, Academy of Sciences, Videnska 1083, 14220 Prague, Czech Republic. E-mail: bures@biomed.cas.cz.

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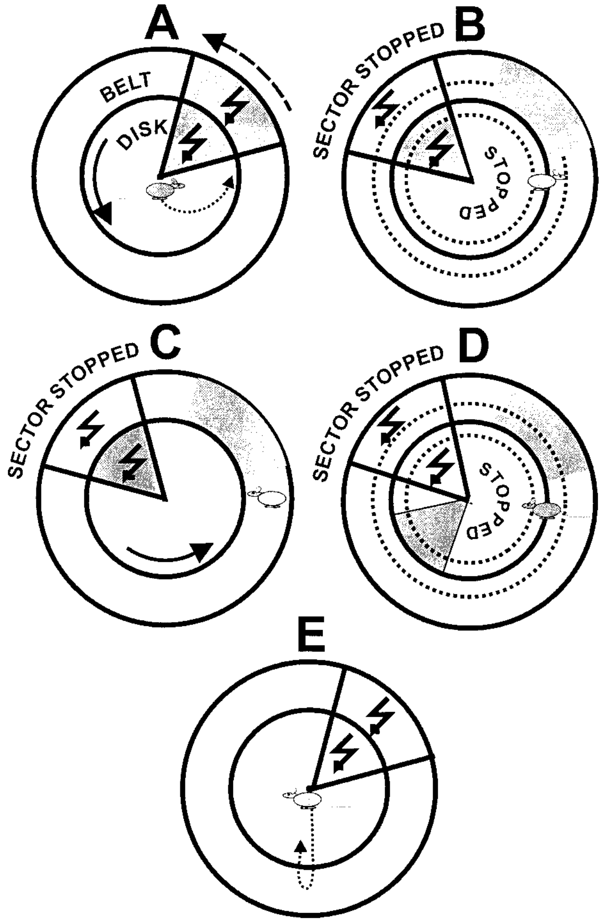

Fig. 1. Schematic representation of one cycle of the shuffling procedure (condition 2). The circular arena consists of a rotatable inner disk and an immobile peripheral belt (DISK and BELT). (*A*) As long as the rat is on the inner part of the arena, the disk slowly rotates (solid arrow) together with the shock sector (zigzag arrow), the rotation of which is indicated by a dashed arrow. The outer part of the shock sector projects to and moves over the stationary belt. The arena surface forming the original location of the shock sector is painted gray. The rat moves from a central part of the arena to the opposite circumference, but the room frame TV camera sees the active locomotion along a radius combined with counterclockwise rotation of the disk as a spiral. (*B*) When the rat approaches the disk–belt border and enters the "transition zone" (denoted by dotted concentric circles), rotation of the disk stops. Note that the punished part of the floor remains the same on the disk but is on a different part of the belt. The radial direction of the track is seen as radial. (*C*) After the rat moves from the transition zone into the outer belt, the disk resumes rotation again (solid arrow), but the punished sector, anchored to the stationary belt, is projected to new areas of the disk surface. The track on fixed belt is seen undistorted. (*D*) Rotation of the disk stops when the animal returns to the transition zone (dotted circles). Note that at this moment the position of the shock sector on the disk has moved to a different part of its floor. The track through the transition zone is undistorted. The return of the rat to the inner disk marks the end of one complete cycle of shuffling and restores the situation shown in *A*. (*E*) Computer-reconstructed locomotion of the rat in the substratal idiothetic frame as seen with a virtual TV camera rotating with the disk, when the rat was on the rotating disk, and as seen with the real camera, when the rat was on the belt or on an immobile disk. Note that the shock sector always remains in the idiothetically correct position with respect to the rat, but the floor areas (dark gray), originally corresponding to the prohibited sector, are dispersed over the arena surface.

Apparatus. An elevated arena (135 cm in diameter) placed 60 cm above the floor in the center of a darkened room (4 × 4 m) consisted of an inner circular disk, 85 cm in diameter, surrounded by a 25-cm-wide outer belt (Fig. 1). The floor was covered with a grounded aluminum wire mesh. The inner disk was motor driven and could be rotated at 180°/min. The peripheral belt was immobile. The disk carried on a long radial arm under the arena an infrared light-emitting diode (LED) visible at the arena circumference. Whereas this LED was used to monitor the rotation of the disk, another infrared LED, fixed between the shoulders of the rat by means of a latex harness, indicated the position of the rat. Both LEDs were detected by an overhead TV camera connected to an interactive custom-made tracking system (20) in the adjacent room. The tracking system consisted of a TV camera that monitored the infrared LEDs and a computer that controlled the motor of the central disk and operated an overhead feeder, delivering to the arena small (≈15 mg) pasta pellets at 10-s intervals. The positions of both LEDs were sampled every 100 ms, and their *x, y* coordinates were used for all calculations. The tracking system could define the shock sector position relative to the room or to the animal's track. The foot shock (50 Hz, 0.3–0.5 mA, 0.5 s) was always delivered between the implanted silver wire and the wire mesh floor 0.2 s after the rat had entered the punished sector and repeated after 2 s in case the rat did not escape.

Procedure. All experiments proceeded in complete darkness. At the beginning of the session, the experimenter placed the rat on the periphery of the inner disk opposite shock sector and then immediately left the room. Four basic paradigms were used:

Condition 1, stable arena: Both parts of the arena were stable, immobile relative to each other and to the room. In this configuration, the rat could navigate with the use of idiothesis supported by any perceptible intramaze and extramaze cues. However, because the arena was placed in a dark and silent room, extramaze cues were considered subliminal. The tracks of rats were thus identical in the room and arena frames as well as in the inertial and substratal idiothetic frames, and so was the position of the punished sector.

Condition 2, disk and belt shuffled: As long as the rat was on the inner disk, the disk was slowly rotating (180°/min) together with the shock sector projecting to and moving over the immobile belt. When the rat entered the outer belt, the inner disk continued to rotate physically, but the shock sector remained stable relative to the belt. After the rat reentered the inner disk, the shape of the shock sector was projected back onto the disk. The shock sector was thus maintained in a position predictable by pure substratal idiothesis that corresponded to the room frame when the animal was on the belt and to the arena frame when the animal was on the rotating disk. Inertial idiothesis supported substratal idiothesis on the belt but competed with it on the rotating disk. Putative intramaze cues on the disk and belt were "shuffled" and could not, therefore, support substratal idiothetic navigation (Fig. 1).

Condition 3, disk shuffled: As long as the rat was on the inner disk, this part was stable (together with the shock sector), but when the rat left for the outer belt, the disk started to rotate. The shock sector was thus always stable with respect to the belt and to the room. Intramaze cues on the inner disk were displaced in the absence of the rat, but on the belt their relationship to the shock sector did not change. The rat was always on the stable surface and was never subjected to passive rotation. The substratal idiothetic frame corresponded to the room frame as well as to the inertial idiothetic frame.

Condition 4, belt shuffled: This condition was the complement of condition 3. While the animal was on the inner disk, the disk rotated together with the shock sector, the projection of which glided over the stationary belt. When the rat left for the belt, the inner disk stopped and remained stable as long as the rat was on the belt. After returning to the disk, the animal found that any local cues remained in the idiothetically expected position, whereas putative cues on the outer belt were displaced during every excursion to the disk. The substratal idiothetic frame corresponded in this case to the arena frame of an intermittently rotating arena. It was supported by intramaze cues on the disk but not on the shuffled surface of the belt. The role of inertial idiothesis was the same as in condition 2.

Transitions from the rotating disk to the stable belt and *vice versa* during conditions 2, 3, and 4 could expose rats to situations where their forelimbs are on a stable substrate and hindlimbs are on a moving substrate. To prevent such disturbing conditions, the tracking program defined a transition zone, a virtual ring that extended 10 cm both centrifugally and centripetally from the disk–belt border (Fig. 1). Once a rat entered the transition zone, the rotation of the disk stopped immediately. The rat's passive movement was thus decelerated when it left and accelerated when it entered the disk. The effect of these transient vestibular stimulations will be discussed later.

Data Analysis and Statistical Procedure. The overall activity of the animal was quantified by measuring the length of the path (DISTANCE) in a session. The number of entrances into the shock area measured the efficiency of the place avoidance. Because the number of entrances was highly correlated with DISTANCE, a normalized parameter (DISTANCE/ENTRANCE) was calculated as DISTANCE divided by the number of entrances per session. The number of additional shocks after each entrance to the punished zone (ADD-ON SHOCKS) measured the inability of the animal to successfully escape from the shock sector. The data were analyzed with paired t tests or ANOVAs with repeated measures, and Tukey's test was used for post hoc comparisons. A probability level of 5% was used as the criterion of significance.

Experiment 1

Recent research (17, 18, 21) demonstrated that rats learn to efficiently avoid an unmarked place on a dark rotating arena. Navigation in the arena frame could be supported by substratal idiothesis and by substratal cues, but not by extramaze cues and inertial idiothesis. Experiment 1 examined the efficiency of place avoidance after all (remote or local) exteroceptive cues had been made irrelevant for the solution of the task by breaking their stable spatial relationship to the punished sector.

Methods. Before place avoidance training began, rats ($n = 8$) were placed for several 30-min sessions on the arena to forage for scattered food pellets. Only rats thoroughly accustomed to the arena were trained to avoid a 60° sector on the stable arena (condition 1) during four consecutive 30-min daily sessions. Afterward, the acquisition of similar place avoidance in a purely substratal substratal idiothetic frame (condition 2) began and lasted for seven consecutive 30-min daily sessions. Subsequently, both conditions alternated daily during 18 30-min sessions to evaluate the performance of rats at an asymptotic stage of performance. Because the data from both consecutive and daily alternated paradigms were essentially similar, only the latter results will be presented in detail.

Results and Discussion. Fig. 2*A* shows a typical track on the fourth day of consecutive place avoidance training on the stable arena. The mean DISTANCE, DISTANCE/ENTRANCE, and ADD-ON SHOCK values were 54.6 ± 6.2 m, 17.7 ± 5.6 m, and 1.0 ± 0.4, respectively. The first shuffling session reduced DISTANCE/ENTRANCE to 5.0 ± 1.0 m and increased both DISTANCE and ADD-ON SHOCKS to 68.0 ± 10.4 m and 9.5 ± 2.5, respectively. These values did not change substantially during the 7 days of condition 2 training. A typical track recorded on the last day of consecutive training is illustrated in Fig. 2*B*. The mean DISTANCE, DISTANCE/ENTRANCE, and ADD-ON SHOCKS values were 69.0 ± 9.0 m, 4.2 ± 0.4, and 15.1 ± 5.1, respectively.

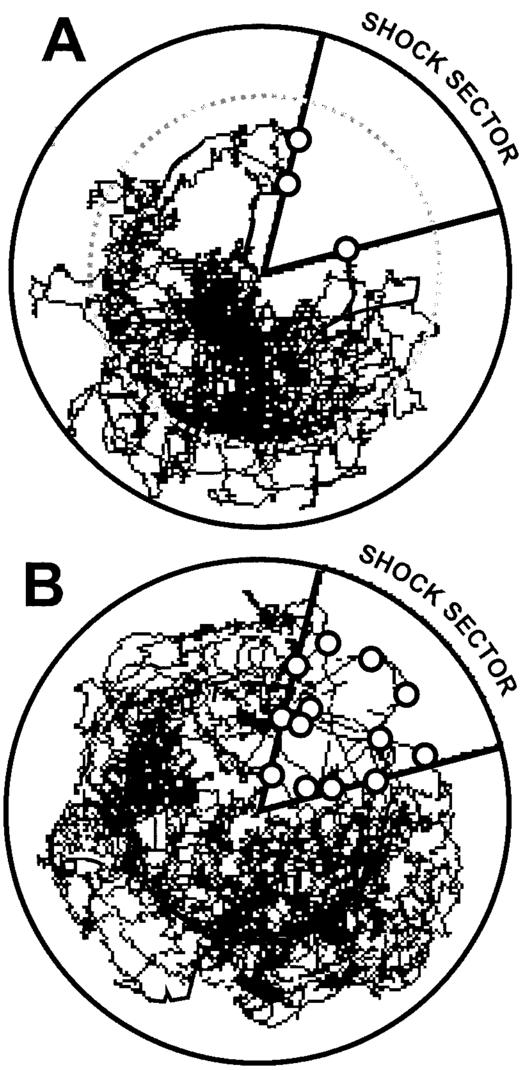

Fig. 2. Example of the tracks of a typical rat on stable (*A*) and shuffled (*B*) arenas. The track in *A* is printed in overlapping arena and room frames, whereas *B* shows the trajectory plotted in the substratal idiothetic frame, reconstructed by the computer from the arena frame segments of track on the disk and room frame segments on the belt. Note that the rat foraged safely on the stable arena (*A*) but committed many errors and failed to rapidly escape from the shock sector on the shuffled arena (*B*). Full circle, contours of the arena; dotted circle, border between the disk and belt; small circles, places of shock delivery.

A prerequisite of effective shuffling is that the animal moves on the shuffled arena in a way that is similar to that of its motion on the stable arena. This prerequisite was assessed by the number of complete transitions between the inner disk and outer belt, which was 16.0 ± 2.3 m on the stable arena and 14.6 ± 2.0 m on the shuffled arena. Shuffling could also affect the incidence of transitions from the inner disk into the transition zone and back into the inner disk. The number of such "incomplete transitions" was 39.3 ± 2.0 on the stable and 31.5 ± 2.2 on the shuffled arena. Paired t test comparison of the above values indicated that shuffling did not change the number of complete transitions, but it reduced the incidence of the incomplete transitions [$t(7) = 2.62$, $P < 0.05$].

Fig. 3 shows the results of 18 alternating presentations of conditions 1 and 2. The mean DISTANCE was lower on the

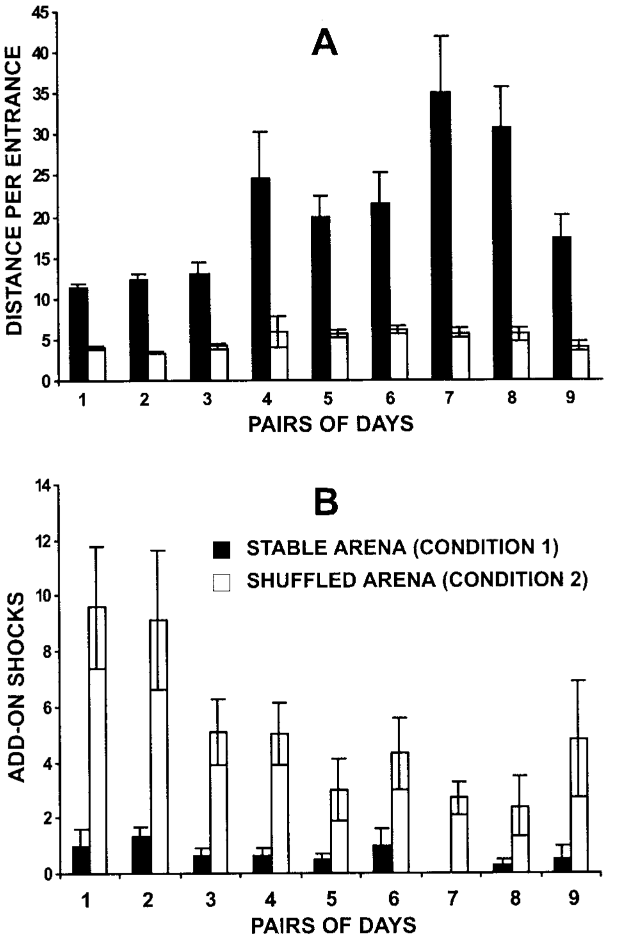

Fig. 3. Place avoidance performance during 18 daily sessions of alternating stable (condition 1) and shuffled (condition 2) arenas. Results are plotted in pairs of days. Black and white columns represent the stable and shuffled arenas, respectively. (*A*) Mean (± SEM) DISTANCE/ENTRANCE in each session. Rats could forage without shock for a significantly shorter distance on a shuffled arena than on a stable arena. (*B*) Mean (± SEM) number of ADD-ON SHOCKS was low during testing on the stable arena and high, but slowly declining, on the shuffled arena.

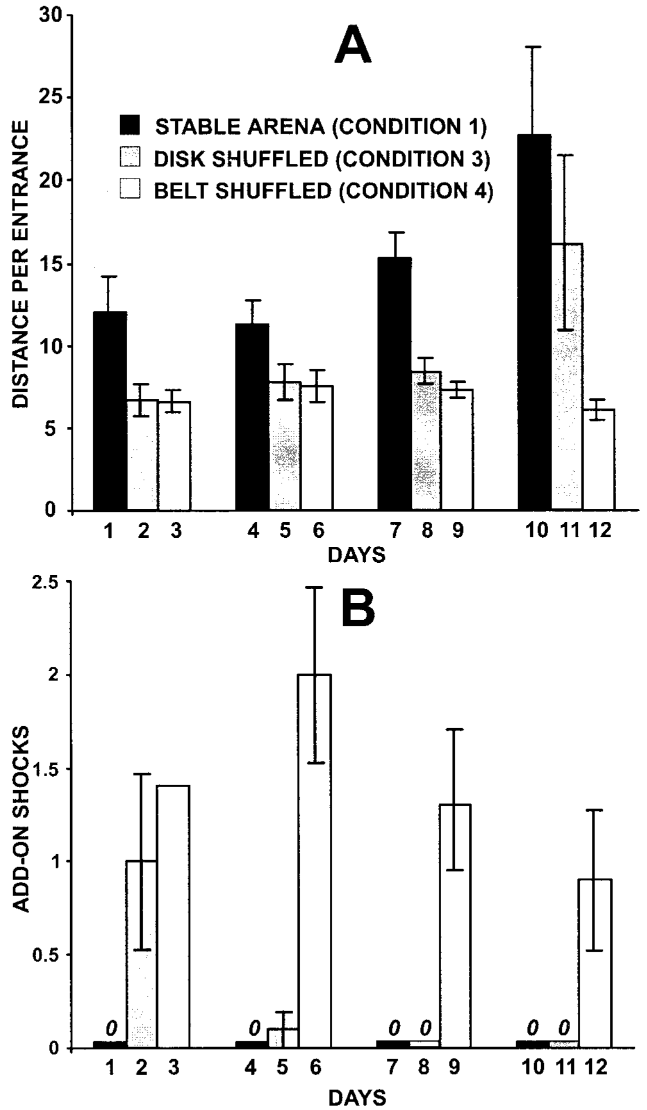

Fig. 4. Place avoidance acquisition during 12 days when condition 1 (stable arena), condition 3 (disk shuffled), and condition 4 (belt shuffled) were changed daily. (*A*) Mean (± SEM) DISTANCE/ENTRANCE. Rats in conditions 3 and 4 are impaired when compared with condition 1, except for the last session, when only the rats in condition 4 are impaired. (*B*) Mean (± SEM) ADD-ON SHOCKS. Note that the rats received no ADD-ON SHOCKS in condition 1, some ADD-ON SHOCKS on the first 2 days, but none in the last 2 days of condition 3. In condition 4, however, some ADD-ON SHOCKS were received in all four sessions.

shuffled arena (54.6 ± 8.3 m) than on the stable arena (82.6 ± 7.0 m). Note that the DISTANCE increased on the stable arena compared with the initial training, which suggests that the rats easily avoided shock in this stable condition. Two-way ANOVA with repeated measures revealed significant effects of days [$F(8,56) = 8.9, P < 0.05$] and condition [$F(1,7) = 106.39, P < 0.01$] but no significant interaction between these factors [$F(8,56) = 1.2, P > 0.05$]. However, the significant effect of days did not reflect any systematic trend; differences between days were just rather variable. The DISTANCE/ENTRANCE was higher on the stable arena than on the shuffled arena (Fig. 3*A*). Two-way ANOVA with repeated measures revealed significant main effects of days [$F(8,56) = 10.12, P < 0.01$] and of conditions [$F(1,7) = 56.55, P < 0.01$] and a significant interaction [$F(8,56 = 2.12, P < 0.05$]. These results demonstrate that the average errorless distance was longer on the stable arena then on the shuffled arena, where performance did not improve despite continued training. The shuffling-induced impairment is better documented by the increase in ADD-ON SHOCKS on the shuffled arena compared with the stable arena. Two-way ANOVA with repeated measures on both factors revealed a significant main effects of days [$F(8,56) = 5.18, P < 0.05$] and of conditions [$F(1,7) = 60.5, P < 0.05$] and significant interaction between these factors [$F(8,56) = 4.18, P < 0.05$]. The interaction demonstrates that the ability to escape from the shock sector improved with prolonged training on the shuffled arena, whereas on the stable arena it was always good (Fig. 3*B*).

The results obtained in experiment 1 demonstrate that place avoidance was severely impaired by devaluation of all intramaze and extramaze cues, which thus could not update substratal idiothesis. This impairment could have been further enhanced by the accelerations and decelerations of passive movements during the disk–belt transitions. Such transitions could confront substratal idiothesis with inertial idiothesis (7, 8). Rats readily acquired efficient place avoidance on the stable arena. After shuffling was introduced, the performance decreased and did not improve in several initial sessions. Once overtrained in the daily alternation paradigm, rats again avoided the shock sector more effectively on a stable than on a shuffled arena. The DISTANCE/ENTRANCE was much shorter on the shuffled arena (condition 2) and did not improve with extended training. The number of ADD-ON SHOCKS gradually decreased with further training on the shuffled arena but did not reach the level attained on the stable arena. This difference in the number of ADD-ON SHOCKS indicates that the incidence of successful escape reactions was improved by prolonged training on the shuffled arena.

Experiment 2

Conditions 3 and 4 were used to assess the interference of substratal idiothesis with inertial idiothesis. In condition 3 (disk shuffled), the rats were not exposed to passive rotations, because the surface of the inner disk was rotated only when the rat was on the outer belt. In contrast, the rats were exposed to passive rotations and corresponding accelerations or decelerations in condition 4, when the surface of the outer belt was dissociated from the shock sector location by rotating the disk when the rat was on it.

Methods. Another group of rats ($n = 7$) was habituated to the arena as in experiment 1. They then acquired place avoidance on the stable arena in six consecutive daily sessions. Afterward, they were trained for 6 days in condition 3 and for 6 days in condition 4. Finally, all three conditions were changed one after the other during the following 12 daily 30-min sessions (Fig. 4).

Results and Discussion. The mean DISTANCE, DISTANCE/ENTRANCE, and ADD-ON SHOCKS values in the last three sessions of the initial consecutive training were 67.8 ± 8.5 m, 17.2 ± 4.7 m, and 0.2 ± 0.2 on the stable arena (condition 1); 59.0 ± 6.9 m, 9.0 ± 2.5 m, and 0.4 ± 0.3 in condition 3 (disk shuffled); and 60.9 ± 4.6 m, 4.3 ± 0.6 m, and 3.7 ± 1.3 in condition 4 (belt shuffled). Whereas the stable arena results did not differ from those obtained in experiment 1, DISTANCE/ENTRANCE was significantly lower in condition 3 than on the stable arena, and this difference was still more pronounced in condition 4.

During alternated training the DISTANCE was lower in conditions 3 and 4 than on the stable arena (64.3 ± 2.2 m on the stable arena, 41.1 ± 1.8 m in condition 3, and 43.8 ± 2.6 m in condition 4). Two-way ANOVA with repeated measures showed a significant main effect of condition [$F(2,12) = 61.2$, $P < 0.05$] but no significant main effect of days [$F(3,18) = 1.8$, $P > 0.05$] and no interaction [$F(6,36) = 1.4$, $P > 0.05$]. Tukey's test revealed that the DISTANCE in condition 1 (stable arena) was longer than in conditions 3 and 4, but no significant difference in DISTANCE was found between conditions 3 and 4. Examination of the DISTANCE/ENTRANCE (Fig. 4*A*) revealed a significant main effect of days [$F(3,18) = 4.12$, $P < 0.05$] and conditions [$F(2,12) = 9.0$, $P < 0.05$], as well as a significant interaction between these factors [$F(6,36) = 3.3$, $P < 0.05$]. Tukey's post hoc test showed that DISTANCE/ENTRANCE was significantly higher in condition 1 (stable arena) than in conditions 3 (disk shuffled) and 4 (belt shuffled), but that this value did not change much between conditions 3 and 4, and that there was a difference between days 1 and 4 and days 2 and 4. ADD-ON SHOCKS (Fig. 4*B*) showed an even more striking difference between the three conditions. Two-way ANOVA with repeated measures on both factors revealed a significant main effect of conditions [$F(2,12) = 49.3$, $P < 0.05$], but no effect of days [$F(3,18) = 1.6$, $P > 0.05$], as well as no interaction [$F(6,36) = 1.8$, $P > 0.05$]. Although the rats received no ADD-ON SHOCKS during the 4 days of testing in the stable arena condition, they received some ADD-ON SHOCKS on the initial 2 days, but not on the last 2 days in condition 3. In condition 4, they received a few ADD-ON SHOCKS on all 4 days of testing.

The number of complete transitions between the inner disk and outer belt during the 12 days of alternated testing was 14.2 ± 1.8 on the stable arena, 16.8 ± 2.3 in condition 3, and 15.4 ± 2.2 in condition 4. The number of incomplete transitions was 34.3 ± 2.5 on the stable arena, 30.0 ± 1.2 in condition 3, and 23.7 ± 1.4 in condition 4. Two-way ANOVA with repeated measures on both factors indicated no significant main effects and no significant interaction for complete transitions. The only relevant result of similar analysis of incomplete transitions was the significant main effect of conditions [$F(2,12) = 3.37$, $P < 0.05$]. *Post hoc* comparisons indicated that the difference in the number of incomplete transitions was significant between conditions 1 and 4 ($P < 0.05$) but not between conditions 1 and 3 or 3 and 4.

The experimental paradigm was modified in experiment 2 to evaluate more precisely the specific factors that can influence place navigation in this task. The activation of inertial idiothesis was eliminated in condition 3 (disk shuffled), but the correspondence of the arena and room frames was preserved. On the other hand, the discordance of the arena and room frames and the exposure of the rat to passive rotations and accelerations/decelerations were features of condition 4 (belt shuffled). The overall locomotor activity was decreased in both conditions 3 and 4 compared with condition 1 (stable arena), suggesting an inhibitory effect of shuffling on foraging. The navigation performance deteriorated in both shuffled conditions (3 and 4) compared with the stable arena, as documented by differences in DISTANCE/ENTRANCE. Impairment in condition 3, when the rats were not subjected to passive rotations, demonstrates that the displacement of the cues on the disk (shuffling) alone impairs place navigation. However, an even more severe impairment in condition 4, documented by an increase in ADD-ON SHOCKS, suggests that passive rotations and the discordance of the arena and room frames with the substratal and inertial idiothetic frames contribute to a further deterioration of navigation.

General Discussion

The aim of the present study was to examine the efficiency of substratal idiothetic navigation over extended periods of time, when all exteroceptive information is made irrelevant for localization of the place to be avoided. At the same time, the avoided place is always stable with respect to the animal's starting position and its path. The principal result is that the place avoidance is significantly impaired by the shuffling procedure, which reduces errorless path integration from about 20 m to 5 m. A similar maximal length of the outward journey compatible with effective path integration homing was reported in golden hamsters (22).

The Shuffling Procedure. The purpose of the shuffling procedure is to simulate locomotion over a fluid substrate by randomizing spatial relationships among floor cues and between these cues and the place to be avoided. The mechanical system allowed the randomization of landmarks along radii, but not within concentric circles. Thus landmarks A on disk and B on belt, which are initially on the same radius, appear on different radii after rotation of the disk. On the other hand, the mutual positions of two landmarks on the disk (belt) are not affected by the rotation. A more efficient randomization of the position of the punished sector with respect to the cues all over the arena surface appears after several disk–belt transitions in condition 2 (Fig. 1).

How Does Shuffling Interfere with Substratal Idiothesis? The present experiments answer this question at different levels. The clearest result is provided by condition 3 (disk shuffled) of experiment 2, which tests the navigation performance of rats in a situation not differing from navigation on a stable arena. The position of the punished sector is stable in the room frame in all parts of the arena entered by the rat. The only difference from condition 1 is that the surface of the disk is shuffled; i.e., when the rat returns from the belt, it does not find the disk cues in the positions predicted by substratal idiothesis.

Reasons for the significantly worse performance of rats trained in condition 4 (belt shuffled) are more complex. This task is an arena frame place avoidance on a rotating but intermittently stopping arena. The position of the punished sector is stable relative to the disk surface but unstable with respect to the belt. Rotation of the disk precludes the use of room frame cues for orientation. The intraarena cues can support substratal idiothetic avoidance only when the rat is on the disk but not when it moves to the shuffled belt. This situation is worse than in the room frame condition 3, where room frame cues can also support substratal idiothetic avoidance on the belt as well as on the disk. Because the room is silent and dark, the main difference between conditions 3 and 4 is probably that inertial idiothesis played a supporting role in the first case and an interfering role in the second case.

The above disturbances are exaggerated in condition 2, when the track is composed of room frame segments (when the rat is on the belt or in the transition zone) and of arena frame segments (when the rat is in the inner part of the disk). Because position of the shock sector is stable neither in the room nor on the arena, substratal idiothesis is updated neither by room frame nor by arena frame cues, but only by delivery of the shock on entrance of the punished sector. Furthermore, the inertial disturbance is enhanced because it now affects not only tracks on the shuffled belt but also tracks on the shuffled disk.

The above analysis reflects the performance of the animals under conditions 1–4. Whereas condition 3 has only a weak disturbing effect, conditions 4 and 2 elicit an equal impairment expressed by DISTANCE/ENTRANCE. The ADD-ON SHOCKS show, however, that condition 2 is significantly more disruptive than condition 4.

What the Rats Should Do but Are Not Doing. The law of effect (23) requires that the animals minimize the effort necessary for obtaining reward or avoiding punishment. In the present experiment, shuffling is fully controlled by the animal which can stop it by remaining either on the disk or on the belt and changing thus the task into the easily learned arena frame or room frame place avoidance. This response may reduce the available reward by 40–60%, but the number of shocks to less than 10%. The fact that the number of disk–belt transitions is not reduced during shuffling indicates that the rats did not recognize the disk–belt transition as the cause of their difficulties or that they did not find the reduced number of shocks a sufficient compensation for the reduced amount of available reward. On the other hand, the reduced number of incomplete transitions, which do not displace the substratal cues supporting the place avoidance during shuffling, indicates that the rats consider them undesirable, probably because they are accompanied by rapid sequences of disk decelerations–accelerations, which may distort substratal idiothesis by activation of the conflicting influence of the inertial input.

Spatial Frames: Are All Real? Fenton *et al.* (21) demonstrated that rats on a rotating arena could simultaneously avoid two places, one in the arena frame and the other in the room frame. The room and arena frames may thus represent some arbitrary spaces for which the animal can create the respective maps that are necessary for efficient navigation. The substratal idiothetic frame, implemented by condition 2, is not identical with room and arena frames, and its failure to support place avoidance may be due not only to the impossibility of updating its compass direction by local and distant cues, but also to the conflicting influence of concomitant activation of inertial idiothesis. The intermediate results of such an interaction of inertial and substratal idiothesis were documented for the gerbil's navigation system (8) and for the rat's head direction cells (24, 25). A more accurate evaluation of the effectiveness of path integration could be achieved with the use of an arena that consists of two independently rotatable parts (disk and belt), which would allow shuffling of the disk while the animal is on the immobile disk and *vice versa*. In experiments with such an arena the shuffling of substratal cues can proceed without exposing animals to rotation.

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